DREDGED MATERIAL RESEARCH PROGRAM

TECHNICAL REPORT D-77-44

COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA

VOLUME I: PRODUCTIVITY

by

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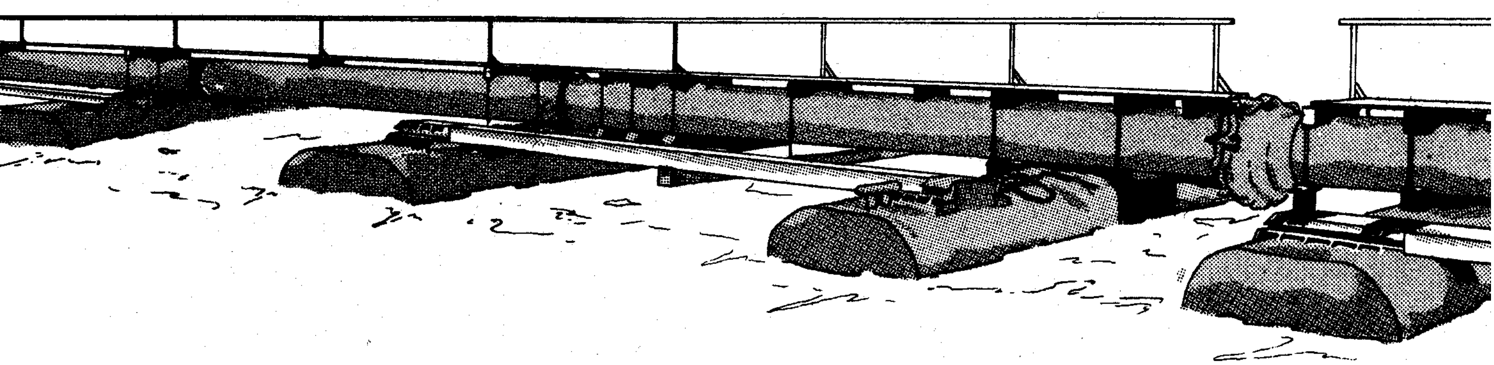

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SUBJECT: Transmittal of Technical Report D-77-44 (2 volumes)

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1. The technical report transmitted herewith represents the results of one of the research efforts (Work Units) under Task 4A (Marsh Development) of the Corps of Engineers' Dredged Material Research Program (DMRP). Task 4A is a part of the Habitat Development Project (HDP) of the DMRP and is concerned with developing, testing, and evaluating the environmental, economic, and engineering feasibility of using dredged material as a substrate for marsh development.

2. The report of Work Unit 4A04B, "Common Marsh Plant Species of the Gulf Coast Area," has been separated into two parts, "Volume I: Productivity" and "Volume II: Growth Dynamics." As indicated by their titles and discussed briefly below, each volume addresses a separate but essential aspect of our knowledge of salt marshes.

3. Net annual aerial primary productivity is a commonly used descriptor of the value of salt marshes and is the subject of Volume I. Primary productivity here is considered the rate at which the sun's energy is stored as plant tissue available to the ecosystem. This work unit deals with several aspects that influence the primary productivity of seven marsh species along the coast of Louisiana. Specifically, the influence of growth habit, turnover rate, climate, salinity, nutrients, and water quality is assessed and comparisons of techniques for measuring productivity are discussed. The information derived in this study should be of direct value in evaluating the relative ecological importance of potential dredged material disposal sites. The information provided will also be exceptionally useful in the design of new marsh habitats on dredged material.

4. Volume II deals with the growth dynamics or physiological ecology of salt marsh species under conditions of stress. Although several species were examined, major emphasis was placed on the substrate selective qualities and adaptation mechanism of *Spartina alterniflora*. The results of this study have been integrated into a general conceptual model that has application to the development of marshes on dredged material.

5. Work Unit 4A04B is one of several research efforts designed by the DMRP to accurately document marsh productivity and the factors that influence the productivity. Closely related work units are 4A04A1, which addresses the productivity of selected marsh species in Louisiana; 4A04A2, which deals with marsh plant substrate selectivity and underground biomass production; and 4A05, in which a simulation model to predict salt marsh productivity was developed. In a less intensive study, Work Unit 4A20 will provide a general evaluation of salt marsh productivity of the Pacific coast of the United States. Additional supportive and comparative data will be forthcoming with the final analysis of the results of field studies at Windmill Point, Virginia, (4A11); Buttermilk Sound, Georgia, (4A12); Apalachicola, Florida, (4A19); and Miller Sands, Oregon, (4B05). Together, these research products provide the Corps with a comprehensive basis for sound management decisions regarding dredged material disposal in salt marsh habitats.

John L. Cannon
JOHN L. CANNON
Colonel, Corps of Engineers
Commander and Director

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20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

As part of the U. S. Army Corps of Engineers Dredged Material Research Program administered by the Environmental Effects Laboratory of the U. S. Army Engineer Waterways Experiment Station in Vicksburg, Mississippi, a study of the productivity of marsh plants common to the Gulf Coast area was conducted.

The study reports on the productivity of seven marsh plant species in coastal marshes of Louisiana. The Wiegert-Evans harvest technique was used to

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20. ABSTRACT (Continued).

measure productivity over a two-year period of the following species: Distichlis spicata (salt grass), Juncus roemerianus (black rush), Phragmites communis (common reed), Spartina alterniflora (saltmarsh cordgrass), Spartina patens (saltmeadow cordgrass), and Sagittaria falcata (bulltongue).

Productivity was found to be related to the growth habit and turnover rate. S. patens, J. roemerianus, and D. spicata were found to be more productive than S. alterniflora, a species that was known to be highly productive. Productivity was higher in the fresh and brackish marsh species than in the salt marsh species and was higher for species that grow throughout the winter than those that die to the ground in late fall.

An evaluation was also made of several techniques for measuring productivity, including harvest, phenometric, and gasometric methods. The study showed that peak standing crop seriously underestimates production in Gulf Coast marshes and that the Wiegert-Evans harvest technique is the most realistic method presently available. This technique includes an estimate of mortality in addition to live biomass changes and so gives the closest estimate of true net aboveground production. The study also showed that phenometric methods have potential as a nondestructive technique that could be developed into a reliable method.

SUMMARY

During the 1955-1964 period disposal of dredged material was a major reason for filling wetlands in the United States. Marsh areas are fairly accessible to many coastal dredging projects and for many years easements were easily obtained and relatively inexpensive; hence, marsh disposal of dredged material improved the cost:benefit ratio that must be applied to federally sponsored engineering projects over other disposal techniques. With the sharp increase in awareness of the value of coastal wetlands as natural systems in recent years, the availability of these areas for disposal of dredged material has decreased and alternatives are being sought. One alternative is to identify tidal wetlands that are of least value in their natural state and thus could serve as possible routes of navigation channels and disposal sites. Perhaps a more viable alternative is the use of dredged material to create new marshes. For both types of disposal the productivity of marsh vegetation and the physiological ecology of stress are important questions.

This study examines the productivity of seven marsh plant species common in coastal marshes of Louisiana (Vol I) and reports on a number of experiments that concern the ability of marsh plants to survive under the dual stresses of salinity and inundation (Vol II). The study was conducted between August 1973 and July 1976 as a portion of the overall DMRP research and development effort under Task 4A, Marsh Development.

Productivity of seven marsh plant species was evaluated over a two-year period. Using a harvesting technique that corrects for mortality between sampling periods, it was determined that *Spartina patens*, *Juncus roemerianus*, and *Distichlis spicata* were even more productive than *Spartina alterniflora*, a species that is known to be highly productive. Measured annual net production (g m^{-2}) was: *S. patens*, 4200; *J. roemerianus*, 3300; *D. spicata*, 2900; *Phragmites communis*, 2400; *Sagittaria falcata*, 2300; *Spartina cynosuroides*, 1100. The fresh and brackish marsh species supported high levels of productivity even though they did not receive as much tidal subsidy as salt marshes. Productivity was higher for species that grow throughout the winter than for those such as

S. cynosuroides and P. communis, which die to the ground in late fall. The broad-leaved fresh marsh species, S. falcata, produced only a moderate level of organic matter, but its high nutrient content (up to 3 percent nitrogen) and rapid decomposition rate made it unique among the species investigated.

Considerable effort was expended evaluating techniques for measurement of production. Peak standing crop was compared with harvest methods that correct for mortality between sampling periods and with nondestructive phenometric techniques based on recruitment, growth, longevity, and density of individual stems. From the evidence it was concluded that peak standing crop seriously underestimates production in gulf coast marshes, and that the harvest technique of Weigert and Evans (1964) is the most realistic presently available, although phenometric analysis holds promise for an excellent, nondestructive method of productivity analysis.

Aside from variation in reported productivity due to differences in techniques, wide geographic variability occurs. High biomass was associated with high silt loads, low organic matter in the sediments, and decreasing salinity.

Soil and tissue nutrient concentrations were also poorly correlated with S. alterniflora biomass. The highest correlation (negative) was between S. alterniflora biomass and boron (B) ($r = -0.32$). Nitrogen (N) was also negatively correlated with biomass ($r = -0.19$). Other significant correlations failed individually to account for as much as 5 percent of the biomass variability. Multiple step-wise regressions were conducted between the dependent variables, S. alterniflora live biomass and total live plus dead biomass, and the independent variables, 14 tissue elements or 8 substrate parameters. The best seven-variable model of tissue nutrients accounted for only 36 to 38 percent of biomass variability. Boron and manganese (Mn) were significant variables in all models. Phosphorus (P), potassium (K), and N also entered the relationship with live biomass, K, and barium (Ba) with total biomass.

No soil parameter accounted for more than 11 percent of biomass variability. The only significant relationship was between salinity and total biomass. Thus, it appears in the complex environment of the salt marsh that many factors contribute to yield.

These field studies were supplemented by controlled tests in the greenhouse and laboratory. In these tests it was documented that S. alterniflora, S. cynosuroides, and D. spicata are all inhibited by salt in the concentration range of their normal habitat. Kinetic studies with the labelled isotope rubidium (Rb) indicated that a mechanism of action of salt was the inhibition of nutrient absorption since Rb absorption was strongly inhibited in the presence of salt.

In situ studies of photosynthesis of whole salt marsh communities showed that the macrophytes (S. alterniflora) accounted for 90-96 percent of the total photosynthesis of the community. The micro-algae found growing on the lower parts of the S. alterniflora culms and on the surface of the sediments accounted for as much as 10 percent of gross production in the winter, but less in the summertime. However, 64-76 percent of the total community respiration was benthic and attributed to the micro-components of the community. The photosynthetic rate increased from shade to full sunlight, a characteristic of C_4 plants (which are particularly efficient photosynthesizers). The rate of photosynthesis per unit leaf area was higher in December and March than during late spring and summer. The decrease in efficiency in late spring was perhaps related to the N supply to the roots. The rate of photosynthesis was not affected by the diurnal flooding pattern of the marsh, apparently because the marsh substrate was efficiently buffered from rapid daily redox potential (Eh) and salinity changes.

These results are discussed in a model of marsh success which identifies several feedback loops that stabilize natural marshes, allowing them to counteract the effects of natural subsidence rates and remain at an elevation just below mean high water level. The inundation regime of the marsh is critical in controlling all of these loops through control of the nutrient and silt supply to the marsh, the salinity of the flooding waters and sediments, and the soil Eh. However, much more needs to be known about the relationship of these factors to the flooding regime.

The relationships discussed in the model are important because they can be used to evaluate how existing data on marsh productivity are interpreted, where dredging and dredged material disposal should occur, and what species and edaphic conditions are optimum for vegetation of newly created marshes.

PREFACE

The work described in this report was performed under contracts DACW39-73-C-0105 entitled "Productivity of Minor Grass Species" and DACW39-73-C-0108 entitled "Physiological Response of Marsh Plants to Environmental Stress," both dated 30 May 1973, between the U.S. Army Engineer Waterways Experiment Station (WES), Environmental Effects Laboratory (EEL), Vicksburg, Miss., and Louisiana State University, Baton Rouge, LA. The research was sponsored by the Dredged Material Research Program (DMRP) under Task 4A, "Marsh Development." The studies included in this report were performed during the period from June 1973 to June 1976.

The research was conducted by Dr. James G. Gosselink, Professor of Marine Sciences; Dr. Roland T. Parrondo, Assistant Professor Botany; and Mr. Charles S. Hopkinson, Research Associate. The main text was written by Dr. Gosselink; Appendix A and B by Mr. Hopkinson, Dr. Gosselink, Dr. Parrondo, and Mr. L. Gulick; and Appendix C by Dr. Parrondo, Mr. E. Bishop, and Mr. Hopkinson. Mr. Pat Cavell, Mr. Lee Grush, Ms. Jean Gosselink, and Ms. Karenlee Kneller were employed to assist with this work. In addition, support from a number of other individuals is acknowledged. Mr. Edwin Bishop, in particular, was responsible for all the technical electronics involved in the photosynthesis studies. Mr. Rodney Adams and Mr. Ralph Cunningham provided reliable field support. Personal communication with Drs. R. J. Reimold and J. L. Gallagher of the University of Georgia was valuable for this report.

The contract was monitored by Dr. C. R. Lee, Ecosystem Processes Research Branch, and Dr. Luther Holloway and Dr. Terry Huffman, Habitat Development Project (HDP), EEL. The study was under the supervision of Dr. Hanley K. Smith, Manager, HDP, and the general supervision of Dr. John Harrison, Chief, EEL.

Directors of WES during the conduct of the study and preparation of the report were COL G. H. Hilt, CE, and COL J. L. Cannon, CE. Technical Director was Mr. F. R. Brown.

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Note: Appendixes A-C were reproduced on microfiche and are enclosed in an envelope attached to the inside of the back cover.

CONTENTS

CONVERSION FACTORS, U. S. CUSTOMARY TO METRIC (SI) UNITS OF MEASUREMENT

U. S. customary units of measurement used in this report can be converted to metric (SI) units as follows:

Multiply	By	To Obtain
miles (U. S. statute)	1.609344	kilometers
acres	4046.856	square meters
cubic yards	0.7645549	cubic meters

VOLUME I: PRODUCTIVITY

INTRODUCTION

Dredging Activities

1. Each year the U.S. Army Corps of Engineers (CE) dredges 300 million cubic yards* of material from the 22,000 miles of navigable waters of the continental U.S.A. (Boyd et al. 1972). Costs for moving this material vary from about twenty cents to several dollars per cubic yard. The distance to the disposal site is a significant factor in the cost, a fact that is critically important for the present study. Dredging to maintain navigation channels is more extensive than any other single dredging activity throughout U.S. estuaries. Even for the highly industrialized and densely populated eastern coast, from 1955 to 1964 disposal of dredged material was the major reason for filling wetlands (Clark 1967). Here, if anywhere, one would expect wetland filling for industrial and residential needs to predominate. Clark indicates that a total of 45,000 acres was filled from 1955 to 1964, of which 34 percent was filled to dispose of dredged material. These areas, used first for dredged material disposal, are often later used for other development projects.

2. The importance of dredging in estuaries to the Nation's economy is indicated by the fact that 132 of the 170 ocean ports in the United States are located in estuaries. These ports handle about 90 percent of the total U.S. foreign trade. In recent years approximately one half of

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* A table of factors for converting U. S. customary units of measurement to metric (SI) can be found on page 9.

the Army Corps of Engineers' budget for maintenance of the Nation's channels and harbors has been for use in coastal areas (Sweet 1971).

3. Thus the use of marshlands as dredged material disposal sites has been a common CE practice for many years. One major reason for this is the cost-benefit ratio that must be applied to federally sponsored engineering projects. The removal of large volumes of dredged material to a disposal site is a significant economic consideration. Marsh areas are fairly accessible to many coastal dredging projects and for many years easements were easily obtainable and relatively inexpensive. In addition these marsh areas have been considered of marginal value (Boyd et al. 1972). Indeed, local interests were often anxious to have marshlands filled because it offered opportunity for future development.

4. In recent years however there has been a sharp increase in awareness of the value of coastal wetlands as natural systems. Because of natural tidal subsidies and the naturally high nutrient levels of most estuaries, wetland productivity is higher than productivity in any terrestrial system. Turner (1976) documented the dependence of coastal fisheries on tidal wetlands. Other studies (Gosselink et al. 1974; Valiella et al. 1975; and Grant and Patrick 1970) have documented the importance of wetlands in tertiary treatment of polluted waters and in the overall global balance of such critical nutrients as nitrogen, phosphorus, and sulfur. As an awareness of the value of natural wetlands has become greater, the availability of these areas for disposal of dredged material has naturally decreased so that coastal wetlands are no longer readily available as disposal grounds. Indeed, the Corps of Engineers itself is readily cognizant of the detrimental effects of disposal on

marshes and is earnestly seeking economically feasible disposal alternatives. At the same time it is realized that because of the magnitude of the dredging necessary to maintain navigable waters in coastal areas, some disposal of dredged material on marshes will continue to be necessary.

5. Through the Dredged Material Research Program (DMRP), the Corps is attacking the problems of disposal of dredged material in coastal zones from a number of different directions. Efforts are being made to identify the tidal wetlands that are of least value in their natural state for possible routes of navigation channels and as disposal sites. Concurrent efforts are identifying methods of minimizing the impact of disposal of dredged material. One of the most viable alternatives to marsh disposal is the positive use of dredged material to create new marshes.

6. For both types of disposal--on existing marshes and by creating new marshes--the question of productivity of marsh vegetation, either existing or to be created, is critical in the response of the ecosystem. Production by marsh plants is the base of the marsh food web. In addition, good evidence from a number of sources (Heald 1969; Teal 1962; and Odum and de la Cruz 1967) indicates that the export of organic matter from tidal marshes is an important food source to consumers (fisheries, shell fisheries, etc.) in estuarine waters. In addition, the extensive root systems of marsh plants are undoubtedly an important factor in stability of sediments. These rooted plants act as traps for fine silt and clay particles in the water column and thus serve to clarify the water and remove materials which otherwise might require

subsequent dredging. For instance, Ambrose, in an article published in 1888 (Coates 1972), described how all of the early harbors on the southeastern coast of England were silted up when the great marshes were first diked and filled. Constant dredging and a vast expenditure of national funds then became necessary to keep harbors operational. These functions and a number of other natural services of the marsh all depend to some extent on the level of primary production of the marsh macrophytes, which are the dominant organisms on the marsh.

7. This study reports the productivity of seven marsh plant species in coastal marshes of Louisiana: *Distichlis spicata* (salt grass), *Juncus roemerianus* (black rush), *Phragmites communis** (common reed), *Spartina alterniflora* (saltmarsh cordgrass), *Spartina cynosuroides* (big cordgrass), *Spartina patens* (saltmeadow cordgrass), and *Sagittaria falcata* (bulltongue). The study was conducted between August 1973 and July 1976. It was designed to satisfy one portion of the overall DMRP research and development effort under Task 4A, Marsh Development.

Problems of Measurement of Primary Production

8. Traditional techniques for measurement of primary production involve harvesting plant material, usually at the end of the growing season when aboveground biomass is maximum. This aboveground biomass, in many studies, has been taken to be equivalent to net aboveground production. Parenthetically, until recently the importance of the root biomass has generally been ignored. Aboveground biomass, it was recognized, contributed to the secondary consumers in the food web but the contribution

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* *Phragmites communis* is a commonly accepted name for the common reed and appears throughout many current literary works; however, the U. S. National Herbarium has recently accepted *P. australis* as the proper name for this grass (Personal Communication, 2 August 1977, Dr. Thomas R. Soderstrom, Agrostologist, Dept. of Botany, Smithsonian Institute, Washington, D. C.

of the roots was not considered. Figure 1 summarizes in diagrammatic form the dynamics of plant growth. In this figure gross production is represented by the flow of materials into the live biomass compartment. Net production, the growth dynamic of most interest in productivity studies, is gross production less plant respiration. The material which accumulates in the live compartment is dissipated by translocation to the roots, by mortality of the plant, and by leaching losses from plant parts. The dead compartment is important in the wetland food web because, as in most grassland systems, nearly all the plant production is processed by the microbial detritus system before it becomes available to higher consumers. Thus in this diagram (Figure 1), the dying grass is shown to accumulate in a compartment in which bacteria and other organisms act as food processors. The dead grass is thus dissipated by respiration and also by loss from the system, either through incorporation into the sediments or by tidal flushing from the marsh surface into adjacent water bodies. There is also a small input of production from the aufwuchs community, which is epiphytic on the lower parts of the culms of the marsh plants.

9. As Figure 1 shows, measurement of production is not as straightforward as measurement of peak shoot biomass would indicate. In order for biomass to be equivalent to production, it is necessary that no live vegetation be present at the beginning of the growing season and that no mortality, translocation to roots, or leaching occurs during the growing season. Under these circumstances all aboveground production accumulates in the live shoot compartment and the peak biomass in that compartment accurately measures net shoot production. It has been

recognized from the work of Wiegert and Evans (1964), and more recently in marshes from Kirby and Gosselink (1976) and Hopkinson and Day (in press), that this is seldom true, especially in southern marshes. Wiegert and Evans showed that significant mortality occurs during the summer in old field systems in Michigan, and Kirby and Gosselink's data indicate that the production of S. alterniflora in Louisiana marshes is at least three times the value of the peak standing crop, because many plants die before the end of the growing season.

10. In this study the Wiegert-Evans (1964) technique was used to measure the production of seven marsh plant species because the method includes an estimate of mortality in addition to live biomass changes. Wiegert and Evans measured the loss rate from the dead compartment. During any time period then, the loss rate plus the change in dead biomass estimates mortality, and mortality plus the change in live shoot biomass sums to true net production.

11. This technique yields much higher production estimates than the majority of those found in the literature, so results by this technique are not directly comparable with other work. In the study reported in the following pages, after one year of field work, the estimated values of net production were so high as to be questionable in the minds of many individuals who have used more traditional techniques. Therefore, to be useful, the technique had to be validated against other techniques. As a result, considerable effort was expended in the development of independent measures of production. Harvest technique results were compared with calculations based on stem density and life histories of individual tagged stems and with measurements of direct

carbon dioxide incorporation in plant tissue. These results are presented in the following pages. Best estimates of production and implications for the DMRP are discussed.

TECHNIQUES*

12. The five basic techniques used to measure marsh plant production fall into three categories: harvest techniques that involve clear-cutting of quadrats of vegetation at regular intervals; phenometric techniques that involve the nondestructive measurement of growth parameters of individual plant stems at intervals; and a gasometric analysis involving the measurement of direct carbon dioxide incorporation and evolution by the plants under study.

Harvest Techniques

13. A summary of harvest techniques follows.

<u>a</u>. Peak live biomass was estimated from the harvest of 0.1- to 1-m^2 quadrats when live biomass was at a maximum. In practice, this time was determined from the bimonthly harvest samples obtained for the following technique.

<u>b</u>. Wiegert-Evans Technique (1964): 0.1- to 1-m^2 quadrats were harvested at eight-week intervals over the two-year period of the study (August 1973 to September 1975). All samples were replicated five times. Vegetation from these plots was separated into live and dead stems, and the dead material on the live shoots was also treated separately. Vegetation was dried at 80°C to constant weight and weighed. Loss rates of dead vegetation were estimated from paired plots; the live vegetation was removed from each plot; the dead vegetation was harvested immediately in one plot and after eight weeks in the second. The loss rate (r) was calculated from the change in the amount of dead vegetation during the interval. The instantaneous loss rate (r = g lost per g dead material per day) was

$$r = \frac{\ln (D_{t_o}/DR_{t_1})}{t_1 - t_o}$$

*Techniques are summarized below; details are given in the Appendixes.

where

D_{t_o} = amount of dead material in the 1st quadrat(s) at time t_o

DR_{t_1} = amount of dead material remaining in the 2nd quadrat(s) at time t_1

From this loss rate the disappearance of dead material (X) during a time interval (Δt) is

$$X = r \times \Delta t \times \frac{D_{t_o} + D_{t_1}}{2}$$

where subscripts indicate the sampling time. Mortality (M) for a sampling interval is

$$M = X + \Delta D$$

where

ΔD = change in dead biomass during the sampling interval

Finally, net production (G) for the sampling interval is

$$G = M + \Delta L$$

where

ΔL = change in live biomass during the sampling interval.

Phenometric Analysis

14. At bimonthly intervals the rate of growth and longevity of culms was determined by following at least 119 individual stems of each species throughout most of their life history. Initially plastic tags were placed around 65 different randomly chosen culms of each species. Every eight weeks 15 additional small young culms were tagged and the height and survival of the previously tagged culms ascertained. Density of stems in height class 0-24 cm, 25-49 cm, 50-99 cm, 100-149 cm, and 150 cm was also determined. In addition, randomly selected samples of each species were cut at ground level, measured to the nearest centimeter for height, dried, and weighed to the nearest 0.01 g. A summary of the phenometric techniques used in this study follows.

a. Williams-Murdoch Technique (1972): This method requires estimates of the ratio of growth to average standing crop (maximum biomass to average biomass) and the mean life span of live culms. The relationship of weight to height was also required. The ratio of growth to average standing crop was

$$(\Sigma\ B_{max/n})/(\Sigma\ \bar{B}/n)$$

where

B_{max} = the maximum weight attained by each stem during its life span

n = number of plants

B = the mean weight of a stem during its life span

$\bar{B} = \Sigma(\bar{b}\times\Delta t)/\Sigma\Delta t$ = the mean weight of a stem during its life span

where

$\bar{b}$ = average weight of a stem between successive measurements

Δt = interval between successive measurements

Annual growth (G) was calculated as follows:

$$G = \bar{L} \times (\Sigma\ B_{max/n})/(\Sigma\ \bar{B}/n) \times \Sigma(\bar{B} \times \Sigma\Delta t)/\Sigma\bar{B}$$

That is, growth ($g \times m^{-2} \times yr^{-1}$) = avg standing crop ($g \times m^{-2}$) × growth/average biomass × frequency/year

where

$\bar{L}$ = annual average standing crop of live vegetation.

b. Mortality Method: This technique used determinations of mortality rates and maximum dry weights of individual culms to estimate annual mortality, which, in a steady-state system, should equal annual production. The generalized equation is:

Mortality = stems dying × mass per stem × stem density

for each time interval and for each size class at time of death. Weight per culm was calculated from height/weight regressions. Mortality was calculated from data from individual tagged culms. Plant death during each eight-week interval was summed for a one-year period to estimate annual mortality.

Gasometric Analysis--Carbon Dioxide Flux

15. An infrared gas analyzer was used to measure the change in carbon dioxide (CO_2) in air flowing through a clear acrylic plastic cuvette that enclosed a 0.075-m^2 area of the salt marsh. Air temperature in the cuvette was controlled as described in Appendix C, and light was controlled over the cuvette by taking advantage of natural variations in cloud cover and by use of black plastic or layers of cheese cloth. The analysis of CO_2 flux is described in detail in Appendix C and in Mooney et al. (1971). Production comparisons reported in this work are for a single species, *S. alterniflora*.

16. Figure 2 shows the sampling sites for the seven species. They are more or less along Bayou Lafourche in either the Barataria or the Terrebonne interdistributory basins in southeast Louisiana; details are reported in Appendix A.

RESULTS: PRODUCTION OF SEVEN MARSH PLANT SPECIES COMPARED BY DIFFERENT TECHNIQUES

Comparison of Techniques

Variation in estimates of net primary production

17. Figure 3 shows annual production estimates from the harvest and phenometric production techniques. The most striking observation about the graph, aside from the very high production levels, is that all the techniques show that peak standing biomass seriously underestimates production. Table 1 shows the relationship of net production to peak live biomass as calculated from different production techniques. With two exceptions values vary from 1.4 to over 4, indicating that peak live biomass always significantly underestimates production. One of the first techniques developed to try to estimate the mortality loss was Smalley's (1959). He was able to correct for an unspecified fraction of mortality. The investigators of this study were able to calculate production by Smalley's technique from harvest data. The comparisons show that on the average Smalley's method was 27 percent lower than the mortality method, 53 percent lower than the Williams-Murdoch method, and 57 percent lower than the Wiegert-Evans paired plot harvesting technique.

18. Only one of the two phenometric techniques, the Williams-Murdoch method, generally agreed well with the Wiegert-Evans technique. On the average the estimates from the Weigert-Evans technique were only 1.3 times higher than the estimates from the Williams-Murdoch technique. For two of the six species, production estimates by the Williams-Murdoch method were higher than when calculated from the Wiegert-Evans

paired plot harvesting technique. In some instances a qualitative judgment allows evaluation of the two methods for a single species. For instance, for _S. falcata_ it was recognized that the sampling interval was too long to measure accurately the loss rate for the Wiegert-Evans technique. The Williams-Murdoch method is probably more realistic for these data. It may be more realistic than Wiegert-Evans for _S. patens_ also. With this species it was extremely difficult to measure loss rates because of the density of the stands and almost recumbent growth habit of the species. The underlined numbers in Table 1 are considered the most reliable estimates of production.

19. Production estimates based on gasometric analysis (that is, CO_2 flux) are difficult to integrate over periods of time that are compatible with harvest techniques. However, for the single species studied by the gasometric technique (_S. alterniflora_), the rates of CO_2 fixation are compatible with the highest estimates of net aboveground production from other techniques. On an hourly basis, and in terms of milligrams of carbon fixed per square meter per hour (making allowances for root production), the Wiegert-Evans technique gives average production rates of about 215 mg C $\times$ m^{-2} $\times$ hr^{-2} compared to rough estimates of net production from CO_2 flux of 250 mg C $\times$ m^{-2} $\times$ hr^{-1} (see Appendix C). Thus all the methods used appear to have values that compare very closely to the values derived from the Wiegert-Evans and Williams-Murdoch techniques.

Turnover rates

20. These results all point to an index of production that should

receive more attention in production studies. This index is the "turnover rate," the relationship of net production to mean live biomass. Used with mean biomass the turnover rate allows one to estimate production. If it can be estimated for a number of species and found to be fairly invariate, it could simplify the field work involved in estimating production. This ratio is probably temperature dependent (see Turner 1976), increasing with decreasing latitude. Thus in the United States it is probably highest in Louisiana marshes and lowest along the New England coast. Data from a concurrent study by Reimold and Gallagher (personal communication 1976) should further clarify the relationship of turnover rate to latitude.

Advantages and Disadvantages of the Different Production Techniques

21. A serious consideration in field tests is the cost of the technique used. Peak live biomass requires a single field sampling trip only, requires no elaborate equipment, and is without doubt the simplest measurement to make. On the other hand, it gives no information about seasonal dynamics and as indicated above seriously underestimates true net production. At the other extreme, the harvest technique of Wiegert and Evans combined with the measurement of loss rates, requires intensive field sampling over at least an annual cycle of growth, and it is costly and time-consuming in terms of manpower. It does not, however, require sophisticated equipment aside from a balance and a drying oven. The technique is valuable far beyond the simple figure of annual production that it produces. If the sampling interval is suitable, it also yields data on the seasonal changes in live and dead biomass and on loss

rates, mortality, and production. The phenometric technique of Williams-Murdoch uses valuable averaging methods that tend to minimize errors and also to minimize the number of individual measurements necessary. However, it does not express any seasonal growth dynamics. The mortality technique does show seasonal dynamics of mortality and this can be important in evaluating the effects of disturbances in marsh ecosystems. As with the Wiegert-Evans method, phenometric techniques also require considerable field sampling and are labor intensive, but equipment needs are again minimal. These techniques, in addition, are nondestructive. It is likely that, with appropriate measurements of growth of individual stems, phenometrics can be developed into a good index of seasonal dynamics of growth as well as mortality.

Annual Production of Seven Marsh Plant Species

22. Table 2 summarizes the best estimates of annual production of the seven species. The "best" estimate is either the Wiegert-Evans or the Williams-Murdoch value, depending on a somewhat subjective evaluation of which method was most appropriate for each species. The most striking feature of this table is the extremely high values for aboveground net production for all species compared with, for instance, *S. alterniflora*, which for many years has been considered to be one of the most productive phanerogams known to man. In comparison with other marsh species for which production has been estimated, however, *S. alterniflora* turns out to be no more productive than *J. roemerianus* or *D. spicata* and far less productive than *S. patens*.

23. The productivity is related to the growth habit of the species in question. The most productive three species—*S. patens*, *J. roemerianus*, and *D. spicata*—are species that have considerable green vegetation year-round and for which the annual curve of live biomass does not show any strong peaks. At the other extreme the least productive species, P. *communis* and *S. cynosuroides*, show a clear seasonal growth curve with no live shoot biomass during the winter and a smooth increase during the spring and summer to a fall peak. The other two species fall between these extremes. *S. falcata* appears to have a single growth cycle, but in reality its turnover and decomposition rates are much more rapid than any other species studied. It was the only broad-leaved plant analyzed. It usually dies back to the ground with any freeze but regrows rapidly from roots so that it undergoes several flushes of growth during the winter season. *S. alterniflora* shows a clear seasonal increase in live biomass followed by a high death rate after flowering in the fall, but it also maintains considerable live biomass throughout the winter.

24. Productivity is related to turnover rate, as indicated by the ratio of production to peak biomass (P/B_{max}). *S. cynosuroides* and *P. communis* have low ratios; those species which grow throughout the winter have high ratios. *S. falcata* has an extremely high ratio. The productivity of *S. patens* was a major surprise in this study. It has been known to have a large standing biomass of live and dead vegetation year-round, but there has been no previous analysis of its productivity. It is highly productive in spite of the fact that it receives no strong tidal subsidy and apparently depends primarily on recycling for

nutrients. *S. patens* is not only very productive, but it is the dominant species in Louisiana wetlands, covering an area of 1,565,743 acres (Chabreck 1972).

IMPLICATIONS FOR DMRP

Role of Primary Production in Marsh Ecosystems

25. This study demonstrates that the primary productivity of all the wetland species investigated is very high compared to published reports of productivity of upland plant species. Thus, although there are differences among species, as a general rule wetland productivity is extremely high. Therefore the decision for location of navigable channels for the placement of dredged material on marshes or for the creation of new marshes should not be based primarily on the net productivity of the species concerned. This is true even though it is understood that primary production describes the energetic potential for the whole ecosystem, so that the magnitude of the energy flows through the rest of the food web is limited by the magnitude of primary production.

26. In addition, however, there are other important considerations:

a. The seasonal dynamics of live and dead vegetation, mortality rates, and disappearance rates are important considerations for developments that impact the marsh ecosystem. For instance, the production of live *S. alterniflora* occurs at its fastest rate during spring and early summer. As Figure 4 shows, a great deal of this organic matter does not die until October and November and is not released or carried into the surrounding waters until the following spring. Thus, any disruption of primary production on a marsh is not felt through the food chain in any significant fashion until the next year. In contrast to this one-year delay in energy flow, the short life spans and rapid decay of *S. falcata* leaves suggests that any impact on this plant species is felt immediately by higher links in the food chain (Figure 5). This should be a consideration in planning and timing of impacts on marsh systems and in assessing the effects of these impacts.

b. The growth habit of the plant is another feature of interest in marsh impact analysis. The contrasting life-style of a plant like S. cynosuroides with a single seasonal growth cycle with that of, for instance, S. patens, which has active growth and mortality throughout the year, dictates different uses for these two species and different approaches to their management (Figure 6). In general, the plant with the year-round growth habit appears to have a higher primary productivity, but also it may be more effective as a stabilizing agent for marsh creation since it maintains an active plant cover all year to help control erosion. All the species studied, however, have perennial root systems that undoubtedly help stabilize the substrate.

c. Not only is the magnitude of primary production a characteristic of interest, but the quality of the vegetation is also of concern in the food web. Unfortunately there is no simple criterion for determining food quality. A rough index of quality might be the nitrogen concentration of the tissue since as this rises the concentration of proteins tends to increase. The comparison of the quality of grasses such as S. patens with a broad-leaved monocot such as S. falcata emphasizes the concept of quality. S. patens tissues have very low nitrogen concentration of about 0.7 percent as compared with values up to 3 percent in S. falcata. The former decays slowly in comparison to the broad-leaved monocot, which disappears nearly as fast as it dies.

d. Nutrient cycling strategies are also important in marsh impact analysis. Seasonally the nitrogen concentration in S. patens is fairly constant at about 0.8 percent, while it varies from 1.7 to 3 percent in S. falcata. These differences in concentration when coupled with very different seasonal variations in biomass yield quite different strategies of nutrient cycling (Figure 7). On the one hand S. patens maintains a large constant standing stock of nitrogen in its aboveground biomass although the concentration of nitrogen is low and the palatability of the biomass as a food source is probably also low. In contrast, although S. falcata has a low aboveground biomass, its total aboveground nitrogen content is about equal to S. patens because of the high tissue concentration. The amount of nutrient per unit area varies seasonally by an order of magnitude. S. falcata disappears very rapidly as it dies so that there is a rapid cycling of nutrients. Observations of S. falcata distribution suggest that it is a pioneer species that thrives in disturbed areas or newly formed freshwater marshes, while S. patens is found in much more stable marshes. This may be related to the difference in its strategy of nutrient cycling.

_e_. A consideration of importance in coastal marshes is the relative amount of production available to higher consumers in the food web. The primary value of tidal marshes to commercial fisheries is thought to be the organic matter exported from these marshes to surrounding waters which becomes available in the nursery grounds of the fishes. The portion of total primary production exported, then, is an important consideration in the value of the marsh. This may be completely independent of the productivity of the marsh species and may depend almost entirely on the frequency and depth of inundation of the marsh. The export of organic matter from _S. alterniflora_ marshes, for instance, is thought to be one third to one half of its total net production (Teal 1962; Hopkinson 1973). On the other hand, as one moves inland in Louisiana and tidal energy is reduced, marsh sediments become increasingly organic, and it is apparent that a large portion of the primary production is being deposited in the sediment rather than being exported. Thus, in terms of their value as a food source for aquatic consumers, inland marshes might be less valuable than marshes that receive high tidal energies.

Recommendations

27. Since a large part of this study was devoted to techniques for the measurement of primary production, suggestions for optimum techniques for measurement of primary production are set forth below. The convergence of several different techniques on a single methodology of measurement to give reliable estimates of net primary aboveground production led to recommending the Wiegert-Evans technique for routine studies of plant productivity. This technique gives estimates of production which are closest to true net aboveground production and, in addition, documents seasonal variation in standing stocks, loss rates, and mortality. The phenometric methods also give hope as a nondestructive technique that could be developed into a reliable method, and it is recommended that some effort be put into development of a reliable phenometric technique that would be less time-consuming than the

Wiegert-Evans method. The cost of carrying out the Wiegert-Evans technique will be too great, in many cases, for that technique to be used. As an alternative it is suggested that as data accumulate (especially from this study and work presently being conducted in Georgia), average turnover rates can be calculated for different latitudes and different growth habits. Knowing this, production can be estimated from mean biomass. The latter can already be estimated fairly accurately from average stand height for *S. alterniflora* (Turner and Gosselink 1975).

28. Two additional factors should be considered in field analyses of this kind. One is attention to seasonal changes in root biomass. Evidence is accumulating that the bulk of the total plant biomass is below ground and there is some indication that production as well is greater below ground than above (Reimold and Gallagher, Georgia study in progress). This is extremely important in considerations involving stability and modification of substrates and cannot be ignored in dredged material research studies. A second factor is quality of productivity. The value of production estimates would be increased by judicious use of some index of quality. It is suggested that routine nitrogen analysis of live and dead tissue could usefully supplement information derived from productivity measurements and allow calculation of turnover rates and dynamics of nutrient cycling.

REFERENCES

Boyd, M. B., R. T. Saucier, J. W. Keeley, R. L. Montgomery, E. D. Brown, D. B. Mathis, and C. J. Guice. 1972. Disposal of dredge spoil. WES Tech. Rept. H-72-8.

Chabreck, R. H. 1972. Vegetation, water, and soil characteristics of the Louisiana coastal region. Louisiana State University, Baton Rouge, La. Agri. Exp. Sta. Bull. No. 664.

Clark, J. 1967. Fish and Man: Conflict in the Atlantic estuaries. Spec. Publ. No. 5, Amer. Littoral Soc., Highlands, N.J.

Coates, D. R., ed. 1972. Environmental Geomorphology and Landscape Conservation, Vol. 1, p. 350 in Benchmark Papers in Geology. Dowden, Hutchinson, and Ross, Stroudsburg, Pa.

Gosselink, J. G., E. P. Odum, and R. M. Pope. 1974. The value of the tidal marsh. Louisiana State University, Baton Rouge, Center for Wetland Resources, Sea Grant Publ. No. LSU-SG-74-03.

Grant, R. R., and R. Patrick. 1970. Marsh plant species, Gulf coast area. Pages 105-123 in Two Studies of Tinicum Marsh. The Conservation Foundation, Washington, D.C.

Heald, E. J. 1969. The production of organic detritus in a south Florida estuary. Ph.D. diss., Univ. of Miami, Coral Gables, Fla.

Hopkinson, C. S. 1973. Oxygen consumption by the streamside intertidal community. M.S. thesis, Louisiana State University, Baton Rouge.

Hopkinson, C. S., and J. W. Day Jr. (In press) A model of the Barataria Bay salt marsh ecosystem. To be included in W. C. Hall and J. W. Day Jr. (eds.), An Introduction to Environmental Modeling. Wiley Interscience Div., N.Y.

Kirby, C. J., and J. G. Gosselink. 1976. Primary production in a Louisiana Gulf coast Spartina alterniflora marsh. Ecol. (in press).

Mooney, H. A., E. L. Dunn, P. T. Harrison, P. A. Morrow, B. Bartholemew, and R. L. Hays. 1971. A mobile laboratory for gas exchange measurements. Photosynthetica 5(2):128-132.

Odum, E. P., and A. A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. Pages 383-388 in G. H. Lauff (ed.), Estuaries. Amer. Assn. Advance Sci. Publ. No. 83.

Smalley, A. E. 1959. The role of two invertebrate populations, *Littorina irrorata* and *Ochelimum fidicinium* in the energy flow of a salt marsh ecosystem. Ph.D. diss., Univ. Georgia, Athens.

Sweet, D. C. 1971. The economic and social importance of estuaries. EPA Water Quality Office, Washington, D.C.

Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecol. 43(14):614-624.

Turner, R. E. 1976. Geographic variations in salt marsh macrophyte production: A review. Univ. Texas, Austin, Contr. Mar. Sci. (in press).

Turner, R. E., and J. G. Gosselink. 1975. A note on standing crops of *Spartina alterniflora* in Texas and Florida. Univ. Texas, Austin, Contr. Mar. Sci. 19:113-118.

Valiela, I., J. M. Teal, and W. J. Sass. 1975. Production and dynamics of salt marsh vegetation and the effects of experimental treatment with sewage sludge. J. Appl. Ecol. 12(3):973-982.

Wiegert, R. G., and F. C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in southeastern Michigan. Ecol. 45(1):49-63.

Williams, R. B., and M. B. Murdoch. 1972. Compartmental analysis of the production of *Juncus roemerianus* in a North Carolina salt marsh. Ches. Sci. 13(2):69-79.

Table 1

Annual Shoot Production of Seven Marsh Species Estimated by Different Techniques, With Relationship to Peak Live Biomass

		Technique					
		Wiegert-Evans		Williams-Murdoch		Mortality	
Species	Peak Live Biomass $g \times m^{-2}$	Production $g \times m^{-2} \times yr^{-1}$	P/B_{max}*	Production $g \times m^{-2} \times yr^{-1}$	P/B_{max}*	Production $g \times m^{-2} \times yr^{-1}$	P/B_{max}*
D. spicata	991	2881**	2.9	1967	2.0	1010	1.0
J. roemerianus	1240	3257	2.6	3295	2.7	1850	1.5
P. communis	990	2364	2.3	--	--	--	--
S. falcata	648	1402	2.2	2310	3.6	1113	1.7
S. alterniflora	754	2178	2.9	1381	1.8	1673	2.2
S. cynosuroides	808	1767	2.2	1134	1.4	398	0.5
S. patens	1376	5812	4.2	4159	3.0	2500	1.8
Mean			2.8±0.7		2.4±0.8		1.5±0.6

*Ratio of production to peak live biomass.
**Underlined numbers are considered the most reliable for a species.

Table 2

Summary of Annual Net Shoot Production

by Seven Marsh Plant Species Grouped by Growth Habit

Single seasonal growth cycle:	Production* $g \times m^{-2} \times yr^{-1}$	P/B_{max}
S. cynosuroides	1100	1.4
P. communis	2400**	2.3
Live biomass all year; growth continues throughout winter:		
D. spicata	2900	2.9
J. roemerianus	3300	2.7
S. alterniflora	2200	2.9
S. patens	4200	3.0
Broad leaved; rapid turnover and decomposition rates:		
S. falcata	2300	3.6

*Best estimate from several methods, rounded to nearest 100 g.
**Probably overestimated because of severe sampling problems.

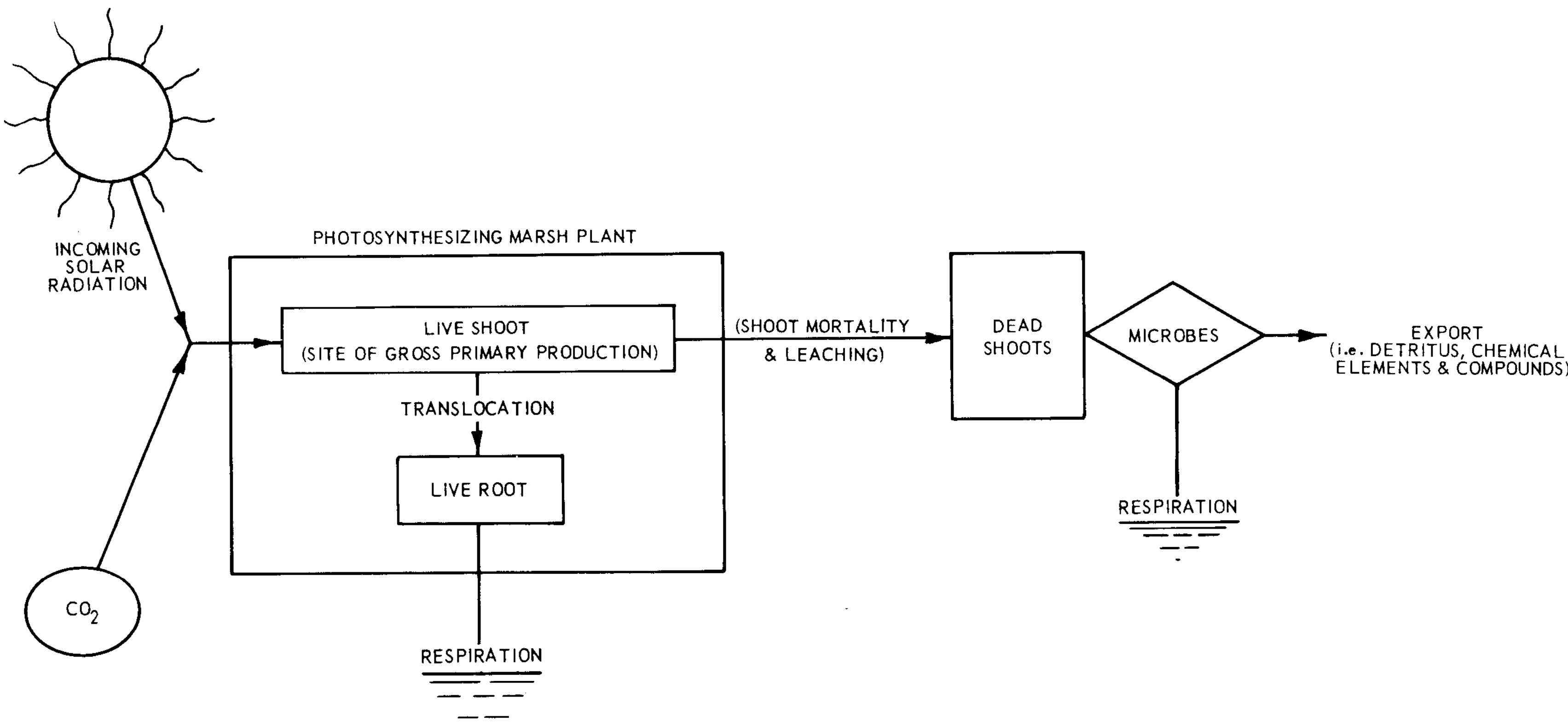

Figure 1. Conceptual model of marsh plant production as it occurs throughout the growing season

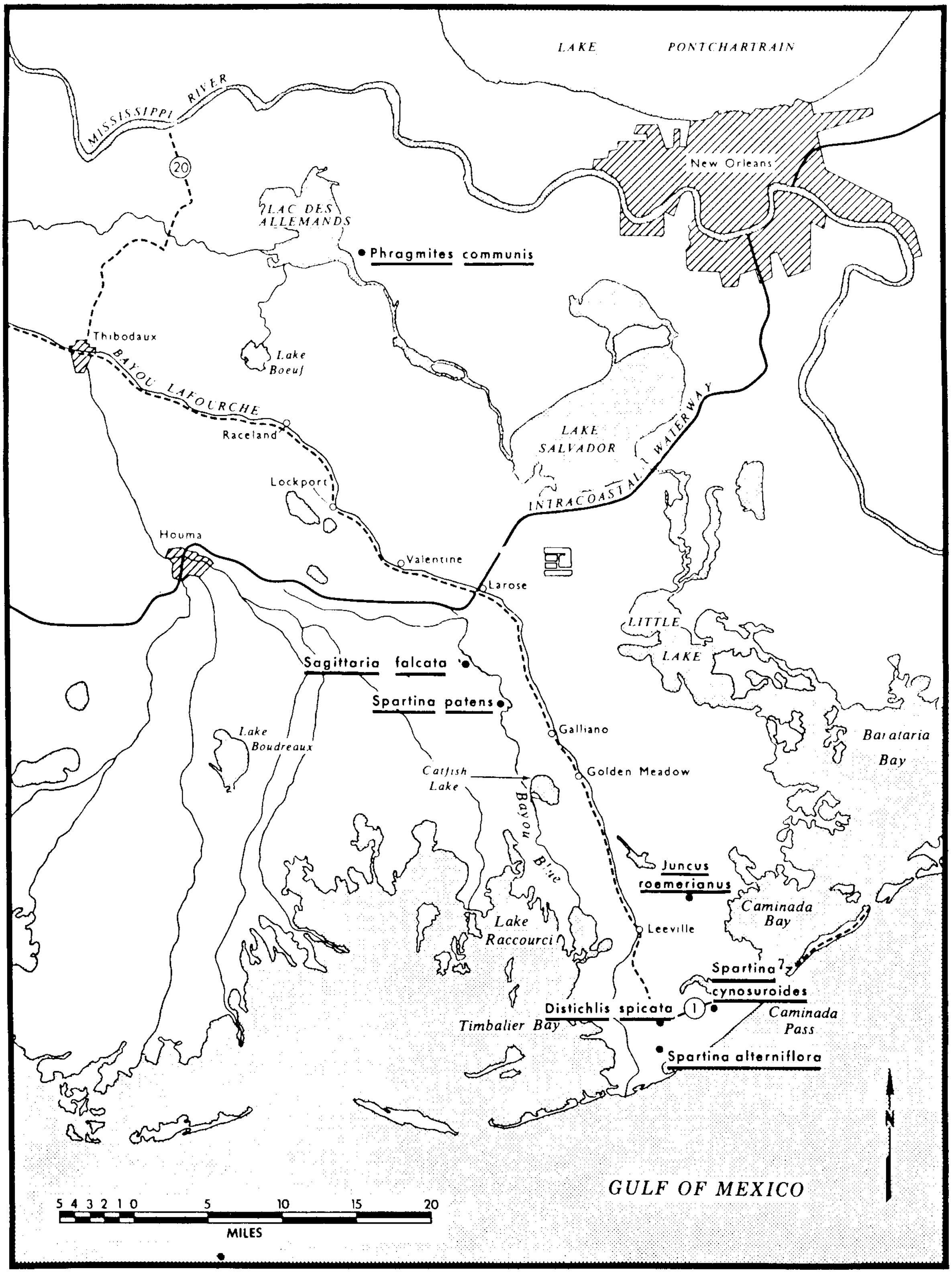

Figure 2. Sampling site locations in southeast Louisiana

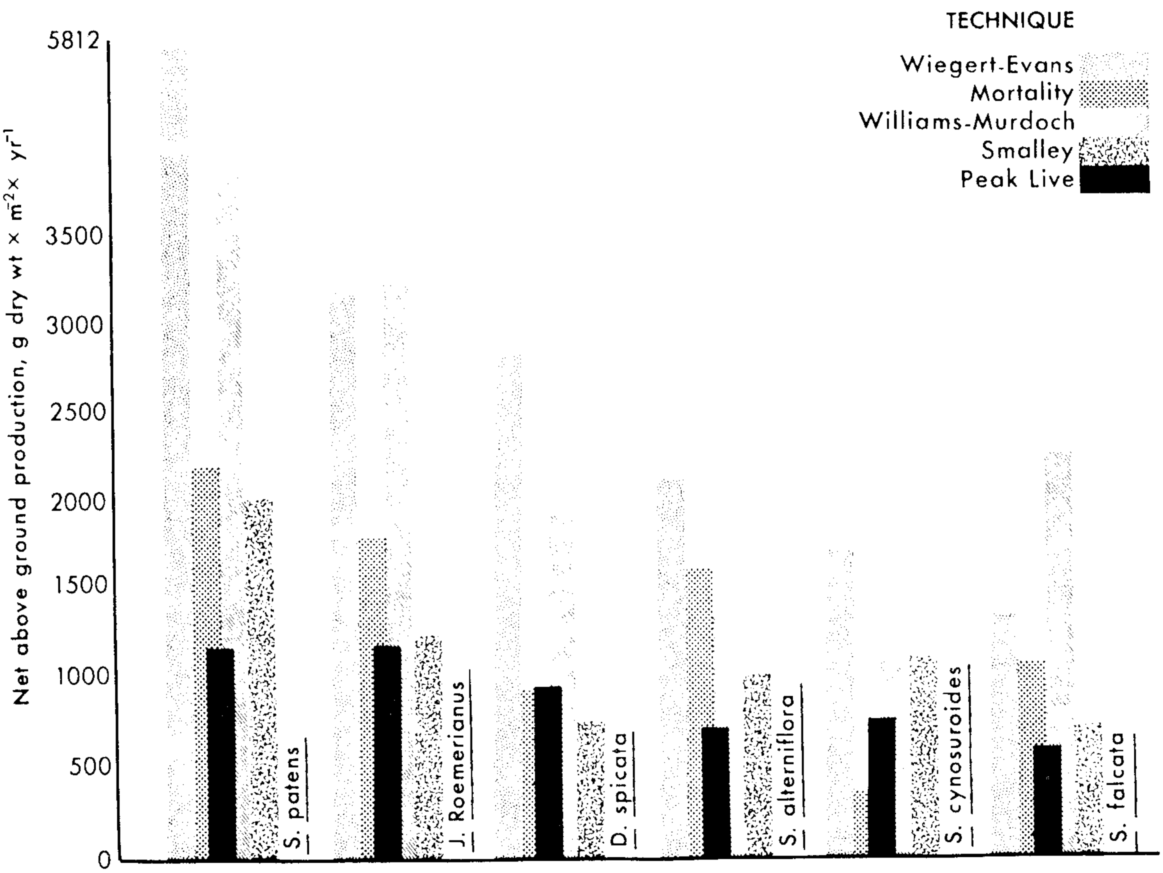

Figure 3. A comparison of production methodologies.

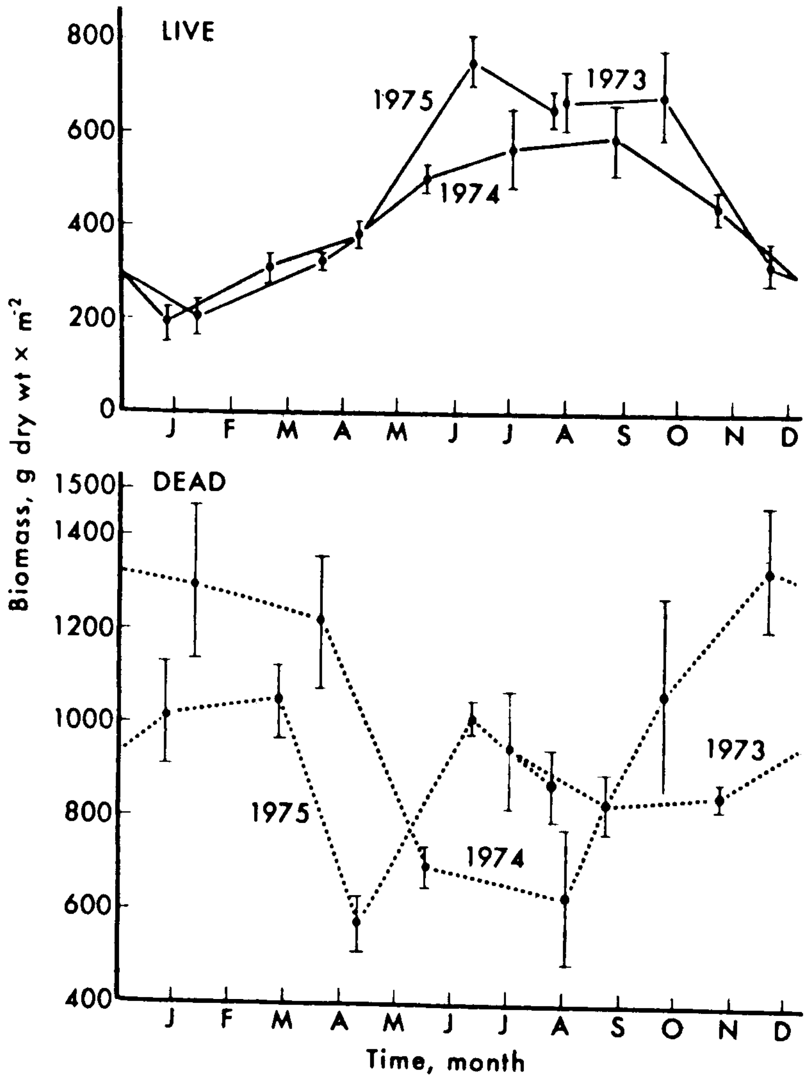

Figure 4. Seasonal changes in live and dead biomass of S. alterniflora.

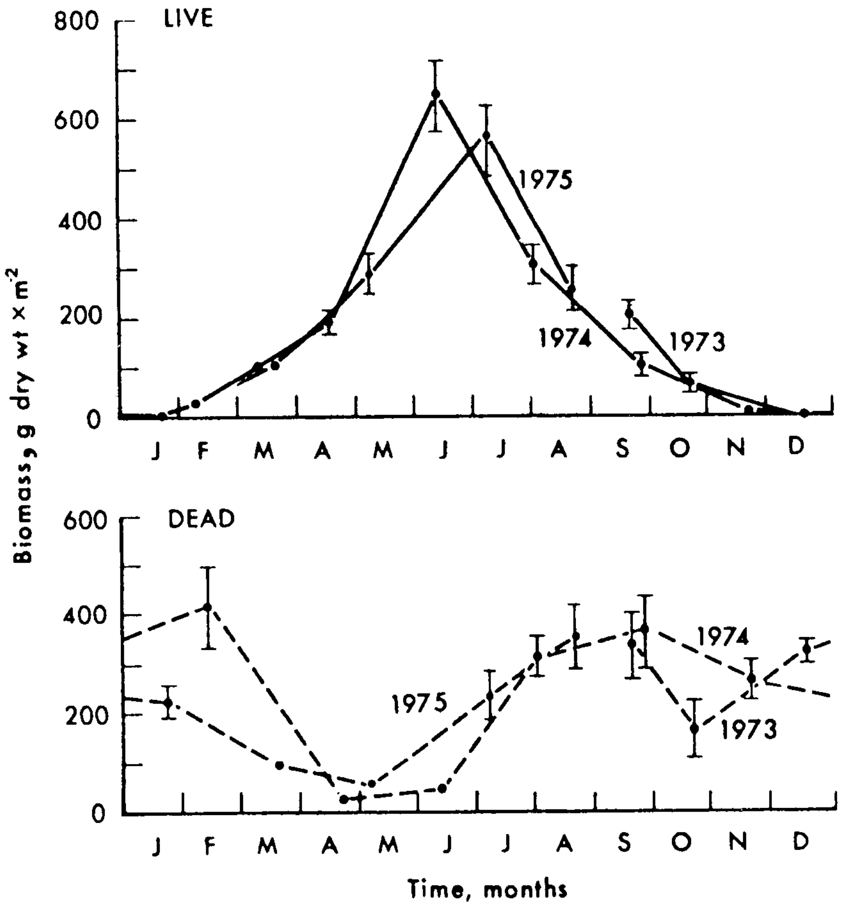

Figure 5. Seasonal changes in live and dead biomass of S. falcata.

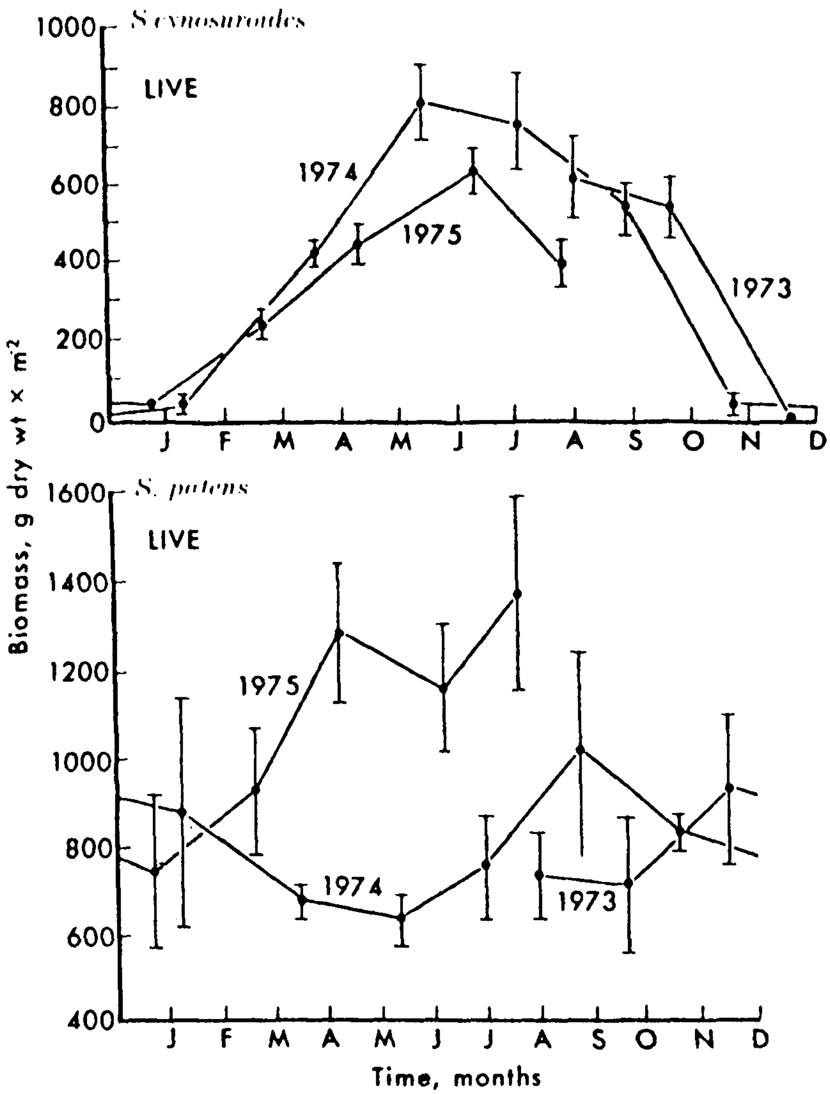

Figure 6. Comparison of the seasonal pattern of live shoot biomass of S. patens and S. cynosuroides.

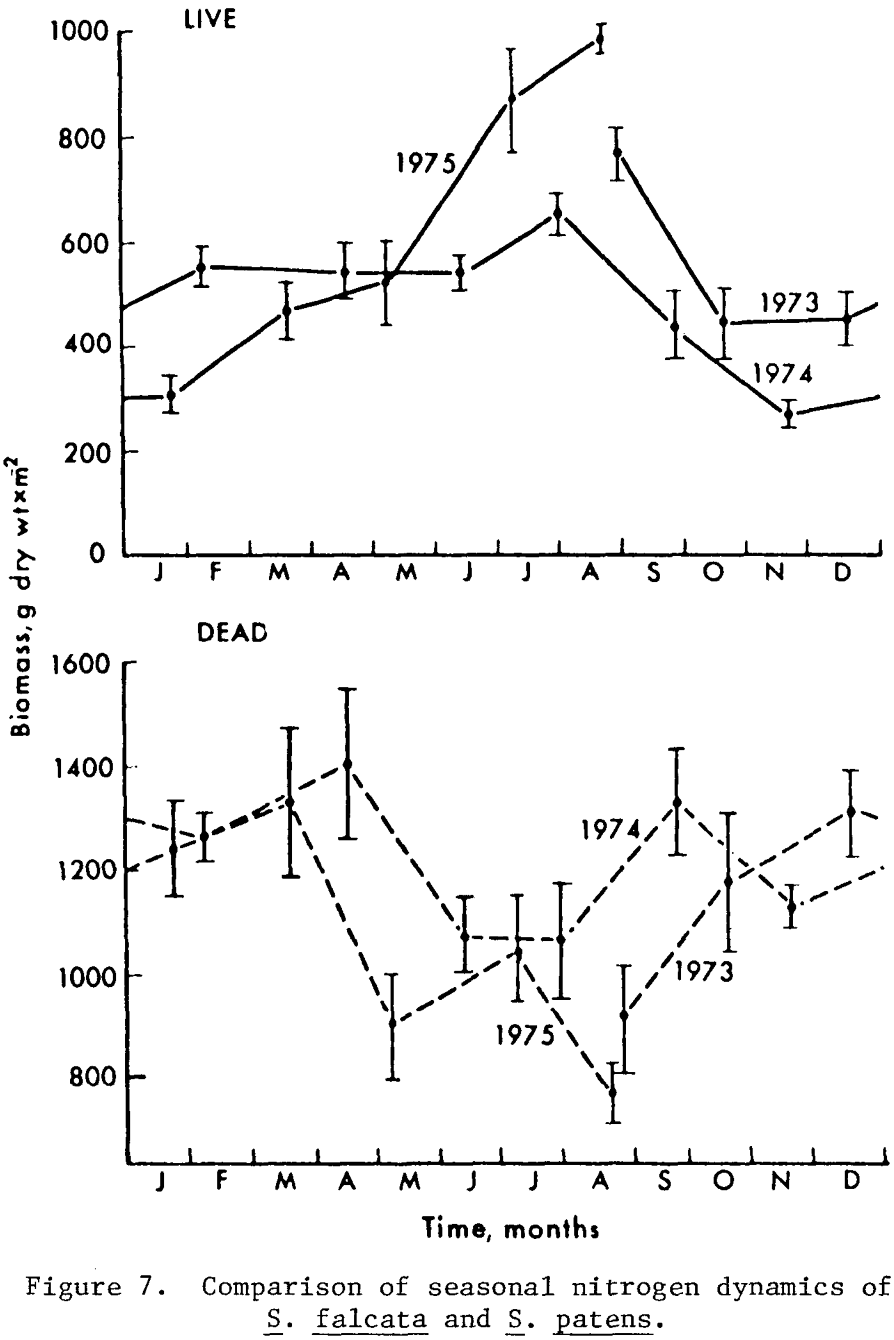

Figure 7. Comparison of seasonal nitrogen dynamics of S. falcata and S. patens.

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Appendixes A-C on microfiche in pocket.

Includes bibliographies.

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